

ADDITIONAL NOTES ON THE VESSELLESS
DICOTYLEDON, AMBORELLA TRICHOPODA BAILL.

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With two plates

IN OUR ORIGINAL INVESTIGATION of *Amborella* (Bailey and Swamy, 1948), the largest stem available was seven millimeters in diameter, obtained from a specimen in the Gray Herbarium, *Vieillard 3149*. Recently, I have received a larger, much older stem from H. S. McKee. The field notes accompanying the specimen are as follows:

"McKee 5617; western slope of Plateau de Dogny, La Foa District, [New Caledonia,] Oct. 25, 1956; shrub 3 to 8 meters high with several stems from common base, some branches pendent especially in older plants; bark light brown, rough; leaves dark glossy green above, slightly lighter below; fruits red. A very common plant between about 600 m. and 800 m." Largest stem seen about 10 cm. in diameter.

The dried section of stem sent to me is asymmetrical in cross section owing to severe injury on one side. It has a large pith 12 mm. in diameter. The longest radius of secondary xylem is 3.5 cm., the shortest 1.6 cm. The bark is very thin, having contracted to approximately one millimeter in thickness. Owing to incipient decay in much of the secondary xylem and to excessive contraction of the bark in drying, it is essential to embed the material in celloidin in order to obtain sections suitable for microscopic study and photomicrography. However, the specimen is of considerable significance, since it enables one to compare the structure of a relatively mature vegetative axis with that of the previously investigated, slender, flowering and fruiting twigs, and to determine that *vessels are absent* in the later-formed xylem of mature stems.

PITH AND BARK

Although the diameter of the pith in McKee's specimen is approximately eight times as broad as that of the slender flowering twigs of *Vieillard 3149* and of other herbarium collections, the structural differences are largely quantitative rather than qualitative. In both cases, the pith is relatively homogeneous, being composed of moderately thick-walled, conspicuously pitted parenchyma and being devoid of idioblasts, nests of stone cells or sclerenchymatous diaphragms. Slender, vertically elongated strands of parenchyma are largely confined to the perimedullary region in close proximity to the elements of the primary xylem.

The softer parts of the secondary phloem in McKee's specimen are badly collapsed and distorted, but the thin-walled parenchymatous cells obviously contained the same dark, amber-colored, colloidal substance that

occurs in the cortex and first-formed phloem of *Vieillard 3149*. However, the later-formed secondary phloem differs from the first-formed phloem in having aggregations of "hippocrepiform" sclereids that appear to have been formed by modification of the cells of the multiseriate rays. There are no fibers in the bark of either young or old stems. Between the outer peridermal layers and the secondary phloem of the large stem, there is a relatively broad zone of a somewhat sclerenchymatous nature. The cells of this layer have moderately and uniformly thickened walls, in contrast to those of the narrow layer of hippocrepiform sclereids that is formed during the early stages of the growth of the stem (compare Bailey and Swamy, 1948, fig. 31). The first-formed narrow zone of sclereids appears to be disrupted during enlargement of a stem, clusters of dissociated hippocrepiform sclereids being incorporated in the subsequently formed broad zone of thick-walled tissue.

XYLEM

The primary xylem of the broad cylindrical eustele of McKee's specimen is distributed in a large number of strands of fluctuating size and conspicuousness (*Fig. 1*). The interfascicular parts of the eustele likewise vary markedly in width and distinctness. In the large stem, as in the slender flowering twigs of Vieillard's collection, there are numerous rents or conspicuous cavities in many of the strands of primary xylem (*Fig. 1*). Without freshly collected and adequately preserved material, it is not possible to determine whether these lacunae form during normal growth and enlargement of a stem or are artifacts produced during the drying and contraction of the vascular tissues.

The rays of the first-formed secondary xylem which extend outward from the fascicular parts of the eustele are uniseriate or biseriate (*Fig. 1*). In addition, there are multiseriate rays which extend outward from conspicuous interfascicular gaps in the eustele (*Fig. 1*). These multiseriate rays vary in number, not only being less numerous in slender flowering twigs, but also being more widely spaced and less numerous in certain parts of the circumference of the McKee specimen than in others (compare *Figs. 1 & 3*). However, in the outermost secondary xylem of the large stem (*Fig. 2*), the multiseriate rays are more abundant and uniformly distributed, their numbers having been augmented in part by enlargement of uniseriate and biseriate rays of the first-formed secondary xylem. The changes in the height and form of the rays and of their constituent cells during lateral enlargement of the stem closely parallels those which have been shown by Barghoorn (1940), Bailey and Howard (1941), and others to occur characteristically in dicotyledonous woods having the primitive, so-called Heterogeneous Type I form of ray structures (Kribs, 1935). In such secondary xylem, both the narrow rays and the multiseriate ones are vertically extensive in the first-formed tissue but become dissected into lower rays during their subsequent extension outward. The elongated cells of the narrow rays maintain their original markedly "erect" orientation except where the rays widen to form multiseriate rays. On the

contrary, the outward extensions of the original multiseriate rays (and of subsequently developing wide rays) are composed of a higher proportion of isodiametric or more or less "procumbent" cells. Although the rays of *Amborella* are of the general primitive heterogeneous form, there are evidences of incipient reduction in the number of multiseriate rays in the first-formed secondary xylem, particularly of slender flowering twigs.

As previously noted (Bailey and Swamy, 1948) the tracheids in the secondary xylem of slender flowering twigs are very long, and obviously are formed as in other primitively vesselless dicotyledons by a primitive type of cambium having long fusiform initials with extensively overlapping ends. The length of the tracheids in the inner and outer parts of the secondary xylem of the McKee specimen are recorded in *Table I*. In each case, the figures given are based upon the measurement of 100 cells.

TABLE 1, SHOWING LENGTH OF TRACHEIDS IN MICRA

	INNERMOST MILLIMETER	OUTERMOST MILLIMETER
Minimum length	1730	1930
Average length	2850	3140
Maximum length	3860	4660

The fusiform cambial initials and tracheids of *Amborella* are of comparable length to those that occur in stems of equivalent diameter of the primitively vesselless dicotyledons, *Tetracentron*, *Trochodendron*, *Sarcandra* and the Winteraceae, and are much longer than those which occur in comparable tissue of vessel-forming dicotyledons. In *Amborella*, the fusiform cambial initials and their tracheary derivatives become longer during increase in circumference of the stem. However, the length of the cells in the outermost part of the McKee specimen is considerably less than that ultimately attained in large stems of arboreal representatives of the Winteraceae, *Tetracentron* and *Trochodendron*. In comparisons between the tracheids of vesselless dicotyledons and gymnosperms it is essential to deal with stems of equivalent ages or diameters; see Bailey and Tupper (1918), Bailey (1920), Bailey (1944), Swamy (1953).

The tracheids of *Amborella*, as seen in transverse section (*Fig. 4*), are characterized by having a strongly angular external outline but their lumina are smoothly circular or oval. This is due to inequalities in the thickness of the secondary wall which tends to be much thicker in the angles of the cells. The bordered pits are restricted to the thinner parts of the radial and tangential walls, being abundantly developed in the radial facets and sporadically and sparsely developed in the tangential ones. A majority of the tracheids have circular bordered pits, 7–10 μ in diameter, in their radial surfaces. In most cases, these pits are arranged uniseriately, but transitions to a biseriate condition are of not infrequent occurrence. Transitions

to scalariform pitting (such as were illustrated by Bailey and Swamy, 1948, fig. 39) are of sporadic and irregular distribution, as in many of the Winteraceae.

Concentric zones of radially narrower tracheids or of wood parenchyma strands occur in parts of McKee's specimen (*Fig. 3*). It is not possible to determine with certainty to what extent these zonal variations may have been induced by injuries in the stem. The distribution of wood parenchyma external to these zones is scanty diffuse.

SUMMARY AND CONCLUSIONS

The chief significance of the McKee specimen is in demonstrating that no vessels are present in the outermost secondary xylem of mature stems, and that the rays of *Amborella* are fundamentally of the primitive Heterogeneous Type I form. It is evident, accordingly, that the cambia and secondary xylem of all of the known primitively vesselless dicotyledons are consistently similar, regardless of whether the plants are small, short-lived shrubs (*Sarcandra*), large shrubs (*Amborella*) or trees (*Tetracentron*, *Trochodendron*, and various representatives of the Winteraceae). In all cases, the cambium is of the long-celled form that occurs throughout the gymnosperms, with the exception of the vessel-forming Gnetales. Wherever vessels appear in the vascular land plants (*Selaginella*, *Pteridium*, Gnetales, monocotyledons and dicotyledons) there is a conspicuous reduction in length of the constituent cells of the xylem. Furthermore, where vessels are eliminated from the secondary xylem of dicotyledons, e.g. certain Cactaceae, and where they are replaced by so-called vascular tracheids, the remaining tracheary cells are short, and the xylem is unlike that of the primitively vesselless gymnosperms and dicotyledons. In addition, it is significant that where such reductions or eliminations occur in extreme xerophytes, aquatics, etc., there are obvious physiological factors involved in their reduction or elimination. Therefore, to assume that the primitively vesselless dicotyledons formerly had vessels and subsequently lost them is purely gratuitous and scientifically unjustifiable.

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EXPLANATION OF PLATES

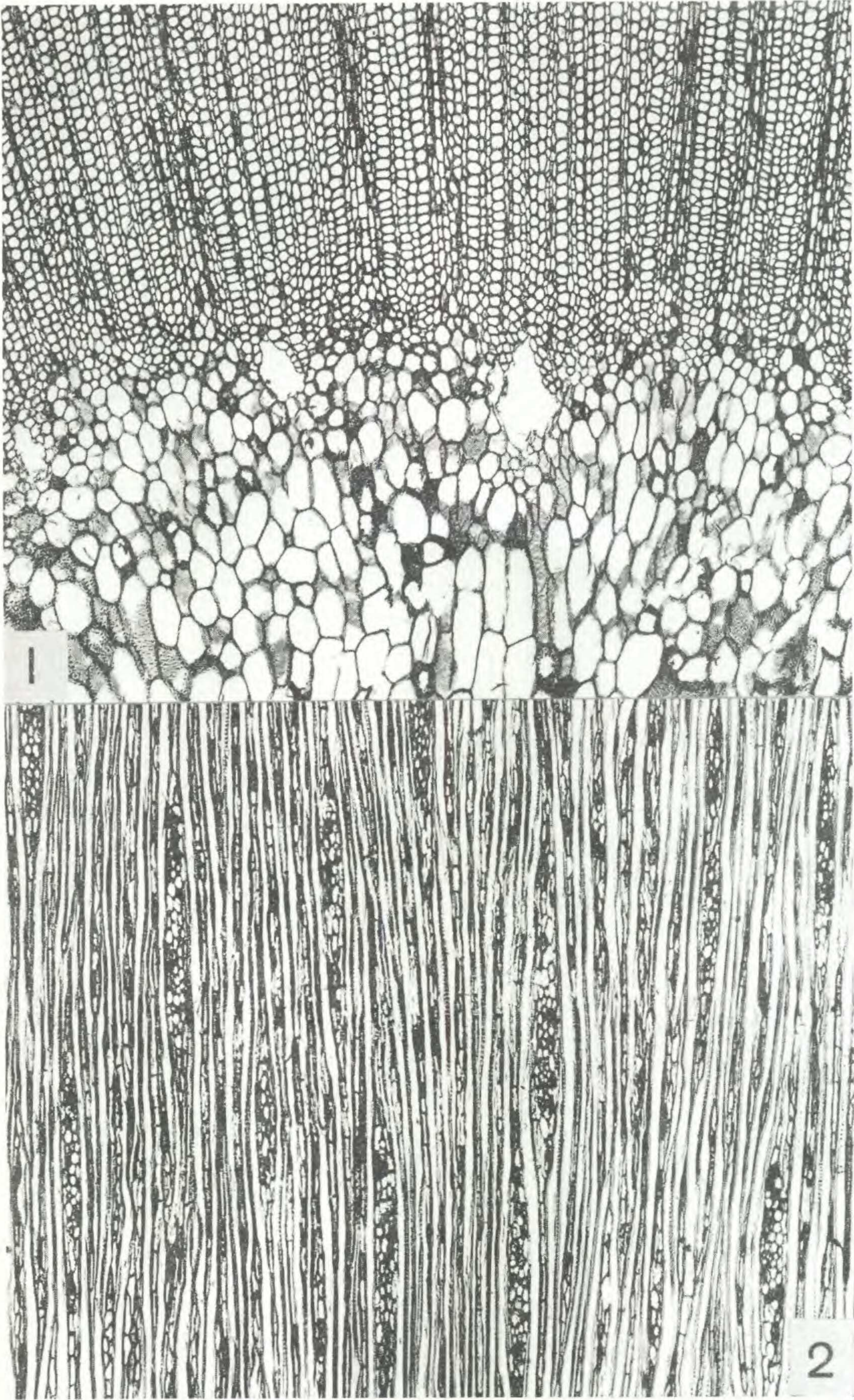
AMBORELLA TRICHOPODA BAILL. (*McKee 5617*).

PLATE I

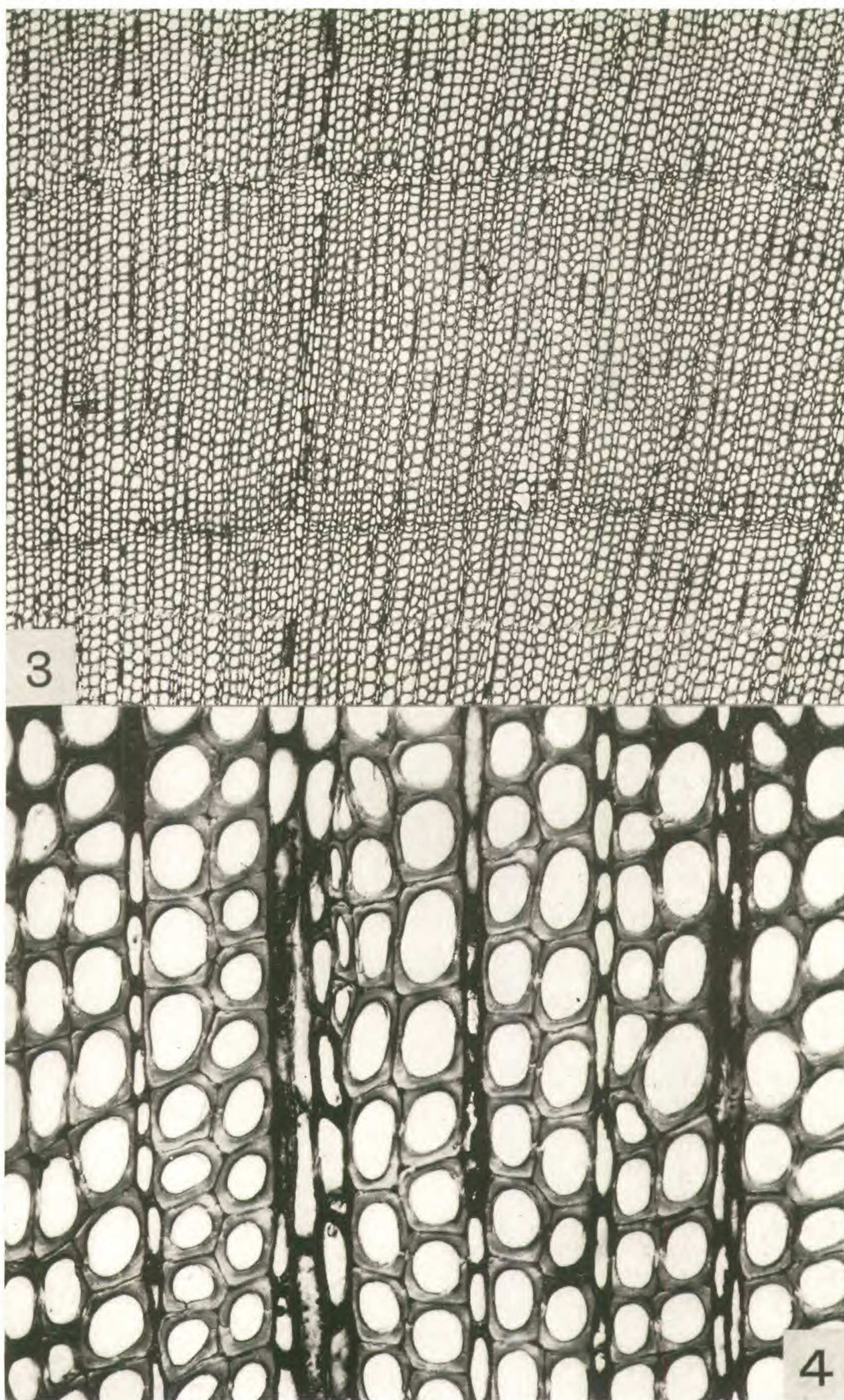
FIG. 1. Transverse section of the stem, showing part of pith and secondary xylem. $\times 40$. FIG. 2. Tangential longitudinal section of the outermost secondary xylem of the stem. $\times 40$.

PLATE II

FIG. 3. Transverse section of the secondary xylem, showing two arcs of wood parenchyma. $\times 40$. FIG. 4. Transverse section of the secondary xylem, showing form of the tracheids in sectional view. $\times 250$.



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